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THE PHYLOGENY OF BACTERIA

By F. D. HEALD

WITH ONE PLATE

The hazy notions which seem to prevail in regard to the light that modern physiology and bacteriological methods throw upon the origin of the smallest of Nature's creation, the bacteria, is the motive which prompts this article. It is a generally conceded fact that any system of classification should be as nearly as possible in harmony with the phylogeny. If this principle is followed it seems quite certain that any scheme of classification which places the bacteria as a sub-class under the artificial group of the Fungi (Vines, 1902) is hardly the proper expression of their position in the plant kingdom. It seems to the author equally absurd to place the bacteria and the Cyanophyceae in a heterogeneous group of poorly defined genera—poorly defined, at least, from the bacteriological standpoint (Cohn, 1875; Bessey, 1904). Neither should I agree with the statement in regard to classification of the bacteria given by Hueppe (Hueppe–Jordan, 1898). "Botanists are almost unanimous in accepting the essential features of the position taken by Cohn, DeBarry, and Hueppe."

The basis for the classification which places genera of bacteria and blue-green algae side by side is the assumption that bacteria are degraded blue-green algae that have lost their chlorophyll and consequently their photosynthetic properties. The assumption is based rather largely upon the similarity of reproduction by fission ("fission algae," "fission fungi"), upon the forms of the cells, and upon the cell-grouping or the cell colonies. Neither these similarities nor some others that may be mentioned appear to be of sufficient weight to justify such an association. The only logical course is to place the bacteria in an independent group parallel with the Cyanophyceae and the various other groups of Thallophyta.

The bacteria are called "fission fungi" even at the present time by various authors. It is needless to discuss the fact that the similarities are purely physiological, and that in the line of the mode of nutrition. That physiological similarities alone are of little value as indicators of genetic development is generally conceded. On the basis of morphological characters the various fungi and the bacteria represent widely divergent forms. The rather ingenious theory of Müller (Müller, 1898) that bacteria originate from the spermatia of various fungi, and that of Hallier (Hallier, 1895), which claims their origin from the plastids of fungus cells, may be mentioned. Notwithstanding the fact that both of these theories are supported by extended laboratory investigations, they must be regarded as the vagaries of distorted imaginations. In recent years some of the true bacteria have been supposed to be simply stages in the growth of a hyphomycete. The discovery of branched forms of the tubercle bacterium, and some others has led to the creation of a new genus, *Mycobacterium* (Chester, 1901; Lehmann-Neuman, 1896). It is extremely doubtful if these branched forms represent normal individuals. They must rather be regarded as crippled and hypertrophied forms of members of the bacillus group, that is, as involution forms (Fischer, 1900). Species of *Streptothrix* which were formerly classed with the bacteria are the only forms which show a similarity to the hyphomycetes and may very properly be excluded from the bacteria.

A much closer relationship appears when we compare the bacteria and that group of the infusoria known as the Flagellata. This is especially prominent in the case of the Erythrobacteria; for example, *Chromatium* and *Rhabdochromatium* bear such striking similarities to some of the Flagellata that it seems almost impossible to separate them. The relationship is still further indicated by the fact that bacteriopurpurin has been found to be identical with the pigment in *Euglena sanguinea,* one of the recognized flagellates (Butschli, 1883). But bacteria in general and the Flagellata appear to show an equally close relationship. Some of the similarities and differences will serve to draw attention to this relationship.

First in the mode of reproduction by fission and the formation of endospores we find a striking similarity. The former is of very much less value than the latter, which is a pronounced morphological character. All bacteria do not produce endospores (only some species of *Bacillus, Bacterium,* and *Spirillum*), neither do all flagellate infusoria produce endogenous resting forms (*Oicomonas, Pleuromonas,* and *Chromulina*), but that method of spore formation is exemplified in both groups, although its details may vary somewhat.

Again, in the comparison of the organs of locomotion the similarity is evident. The types of flagellation in the bacteria find a parallel in nearly every case among the Flagellata. The polar arrangement of the flagella, as in *Pseudomonas, Microspira,* and *Spirillum,* where we find one, two, or a tuft, is a common arrangement for many flagellates. Thus, *Oicomonas* has one polar flagellum, *Bodo, Chilomonas, Cryptomonas* and others have two, while *Tetramitus* has four. The peritrichous type of arrangement of the flagella characteristic for *Bacillus* is paralleled by *Multicilia* for the Flagellata. A third similarity or agreement that is worthy of mention is the character of the external membrane of the cell. The nitrogenous character of the cell wall or cell membrane in bacteria is unique among plants. The so-called "cuticle" of the infusoria is nitrogenous in character, but is not a definite membrane from which the protoplasm can be separated by plasmolysis as in the case of the bacterial cells; it is only the modified external layer of the cell protoplasm.

The main differences that should be noted between the bacteria and these low forms of animal life are in the cell contents. In all except a very few of the flagellate infusoria that are either marine or parasitic, a contractile vacuole is a characteristic structure; no such feature has ever been observed in any bacterial cells, although non-contractile vacuoles may be noted in some of the larger forms. A nucleus is a constant structural element in the Flagellata, while such a structure is never present in a true bacterial cell.

In the matter of nutrition we find many striking parallels between the bacteria and the flagellates. Very great emphasis should not be laid on the similarities of nutrition, but they may at least be mentioned. The discovery of chemosynthetic flagellates is not beyond the realm of probability and will only serve to intensify the fairly well pronounced morphological relationships, as it seems that such forms would be nearer the ancestral type, at least as far as their nutrition is concerned.

Some of our present day botanists make the statement without reserve that bacteria are degenerate and degraded blue-green algae, absolutely excluding the possibility of their independent origin. Before the discovery of the chemosynthetic type of carbohydrate manufacture such an unqualified assumption would have been excusable, and even fairly probable, but in the light of these recent advances in the nutrition of certain soil bacteria (*Micrococcus nitrosus, Pseudomonas europea, Bacterium nitrobacter*), the independent development of the bacteria, especially of the Haplobacteria, seems highly probable.

A fairly close analysis of some of the morphological and structural characteristics of the bacteria and the Cyanophyceae might still leave some doubts as to their relationship, if chemosynthetic food manufacture were unknown. A brief review of the differences as well as the similiarities of the two groups brings out very suggestive, but not conclusive, evidence. First, as regards the internal structure and organization of the protoplasmic cell contents. The most perfected cytological methods have failed to reveal the presence of a nucleus in any bacterial cell, notwithstanding the fact that several investigators of prominence have made claims in that direction (Butschli, 1896; Fischer, 1897), and until recently the majority of evidence was in favor of a similar condition in the blue-green algae. Some recent exhaustive work (Kohl, 1903; Olive, 1904), however, renders this supposed similarity more unlikely, since both authors claim to have discovered a distinct nuclear structure in many of the Cyanophyceae. This nucleus, if present (Fischer, 1905), is of a primitive type and may well be taken to represent one of the first steps in the evolution of the typical structure. The bacterial organism, occupying a lower rung in the ladder of life, has not yet risen to the point where such a morphological differentiation has become necessary in the life of the cell. If the nucleate cell is the true morphological conception of the blue-green algae, it appears difficult to understand how the adoption of a different mode of nutrition has caused the disappearance of the nucleus, as would be necessary if the bacteria are really degraded blue-green algae. The above-mentioned conception of the bacterial cell as a more primitive form, seems to the author to be much more probable. Parasitism or saprophytism does not lead in other cases to a disappearance of the nucleus, although it may lead to its diminution in size.

The mode of spore formation is one of the fallen strongholds of the advocates of the degeneration or degradation from the Cyanophyceae. The common production of arthrospores by various species of the two groups was regarded as one of the strong links in the chain of evidence. The pathway of science is strewn with the wrecks of discarded hypotheses and erroneous observations, and here is no exception. Although we find noted investigators (De-Bary, 1884, 1887; Hueppe–Jordan, 1899) as champions of the arthrospore theory for bacteria, the general consensus of opinion among modern bacteriologists is that their observations were the result of distorted imaginations or a misinterpretation of what they actually saw. The fact that some of the Cyanophyceae form resting spores from certain cells of a filament was quite probably the guiding impulse in the discovery of the so-called "arthrospores" in bacteria. The only bacterium in which arthrospore formation is at all probable is *Streptothrix mesenteroides.*[1] Granting, then, that the arthrospore is a delusion (Fischer, 1900), the similarity of spore reproduction has disappeared, since none of the blue-green algae form endospores. It would seem rather difficult to understand how these poor degraded blue-green algae have either gained or retained the power of producing endospores while their more specialized and normal progenitors have either lost or never acquired the power. This condition of spore formation is perfectly intelligible if we assume an independent origin of the bacteria and the blue-green algae from a common primitive ancestor. It is suggestive to note in this connection that the formation of the so-called "aplanospores" by some of the Chlorophyceae offers a certain morphological similarity to the production of endospores by bacteria.

The common method of vegetative reproduction by fission in bacteria and Cyanophyceae is no argument for the origin of bacteria from blue-green algae ancestors. It may be one of the links in the chain of evidence, but it is rather frail. This common method of propagation is no more an indication of relationship than it is of a degradation from the Protococcoideae among the Chlorophyceae, where a similar propagation prevails as the primitive type, in addition to analogous, if not homologous, cell forms.

A comparison of the two groups in regard to motility indicates a rather close relationship between some of the Trichobacteria and certain of the blue-green algae. Species of *Beggiatoa* and *Oscillatoria* offer a striking similarity, not only from the morphological standpoint, but from their peculiar oscillating and progressive movements. In general the *Leptothrix* forms are quite similar to the Oscillatoriaceae. On the other hand, when the Haplobacteria are considered, we find motile and non-motile forms among coccus, bacillus, and spirillum groups that are actively motile because of the development of special organs of locomotion, the flagella; but in the motile Cyanophyceae, no special organs are developed, only the peculiar and unexplained oscillating or gliding movements being exhibited. If the Haplobacteria are degenerate Cyanophyceae, it is a peculiar case of degradation that has resulted in such a remarkable degree of specialization in the production of monotrichous, lophotrichous, and peritrichous forms. Such an idea is certainly not in harmony with the much more evident cases of degenerate forms.

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[1] The spore formation in *Crenothrix* and *Cladothrix* is not included in this statement.

In the character of the cell walls we find a similarity which is rather largely due to similar physical properties, while from the side of chemical composition a difference must be noted. The more or less mucilaginous modification of the cell wall in the Cyanophyceae is a prominent character, and compared with the zoogloea formation by many of the bacteria has been used as an important feature in indicating relationship. It should be noted that many of the Protococcoideae among the Chlorophyceae also show a mucilaginous modification of their walls. If, instead of laying emphasis on the similar physical properties of the modified wall, we consider the chemical differences, a considerable divergence is indicated. The normal wall in bacteria is unique among plants in being of the nature of a proteid, while in the blue-green and other algae it is a carbohydrate (cellulose). In the modified walls or the jelly masses the same chemical differences prevail in probably the majority of cases. It is true that in some cases it has been claimed that bacteria form cellulose walls, and also that the jelly masses are of a carbohydrate nature (Migula, 1897). Even if the statements are reliable, the great bulk of something like one thousand species never rise to that distinction. It may be that degeneration would result in the loss of power to form a cellulose or even of any kind of a carbohydrate wall, but it does not seem to me that it would operate in that way. At least if this were true, we might reasonably expect to find more of these poor degenerates that had not yet been degraded to the nitrogenous level.

The main stronghold of the advocates of the degradation of the blue-green algae is apparently the similarity of external forms and cell grouping in the supposedly related forms. It seems to me that this apparent similarity has been allowed greater value as an indicator of relationship than is really justifiable. However, before mentioning in some detail these similarities, it should be remembered that almost analogous forms may be selected from the Chlorophyceae. In the first place, it should be kept in mind that the coccus or globular forms, and the rod or cylindrical forms, of the cells are the most easily assumed and normal forms for free cells. Also the simplest possible unions of cells are filaments, or linear aggregates, cell-plates or superficial aggregates, and cell-packets or cell-masses.

The morphological similarities of the bacteria and the blue-green algae have been dwelt upon more or less since the time of Cohn, and there seem to be botanists at the present who consider these similarities all-sufficient in determining the line of descent. Beginning with the coccus forms we may compare *Micrococcus* and *Aphanocapsa,* the cell division taking place in three planes, but forming irregular masses. The diplococcus forms are quite closely simulated by a form like *Syncchocystis aquatilis.* Again, the tetrad forms of *Micrococcus* and *Placoma* and *Merismopedia* agree in the formation of groups of four cells, although distinct colonies are formed by the algae, hollow irregular colonies by *Placoma,* and cell-plates by *Merismopedia.* The colorless relatives never form distinct colonies. *Streptococcus* forms and many of the Nostocaceae, for example *Anabaena,* present a striking similarity. The morphological similarities of *Nostoc* and *Streptococcus mesenteroides* are even more pronounced. Although we find among the Cyanophyceae such forms as *Gloeocapsa, Gomphosphaeria,* and *Microcystis,* in which the cell division takes place in three planes with the formation of colonies of cells, none that form definite cubical packets like *Sarcina* have ever been recorded. It may be of interest to note in this connection that such a form has recently been discovered by Shantz in his plankton studies of Colorado lakes.[1] Those who regard the bacteria as degraded blue-green algae will welcome this as the long-looked-for *Sarcina* form and will place it as another link in the chain of morphological evidence.

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[1] The form has not yet been published.

Considering next the bacillus forms of the bacteria, it may be noted that *Aphanothece* resembles quite closely many of the zoogloea-forming rod bacteria. *Gloeothece* may be compared with the capsule-forming species of *Bacillus* and *Bacterium.*

Cells or cell-filaments showing the spiral form are found in the two groups, although the differences are somewhat greater than similarities of external form would indicate. It is quite suggestive to compare the more or less curved species of *Dactylococcopsis* with species of *Spirosoma;* also *Spirulina* and *Arthrospira* with *Spirillum* and *Spirochaeta.* It is certainly a possibility that these similarities indicate a definite genetic relationship, but the value of such a comparison is somewhat lessened by the fact that quite striking parallels may be found in the more primitive Chlorophyceae.

If the Trichobacteria alone could be considered the degradation hypothesis might still remain unshaken, for *Beggiatoa* and *Oscillatoria, Cladothrix* and *Scytonema, Crenothrix* and *Tolypothrix* show a remarkable similarity. The corespondence is equally pronounced between *Phragmidiothrix* and *Chamaesiphon.*

The differences between the Haplobacteria and some of the Protococcoideae are but little more pronounced than the differences between the same forms and the blue-green algae, while similarities of morphological characters are manifest although perhaps to a less degree. If there were no blue-green algae, it would not be long until some Cohnian systematist would have such forms as *Tetraspora, Palmella, Apiocystis,* and *Pleurococcus* arrayed with the coccus forms of the bacteria.[1] The relationship of the rod-bacteria (*Bacillus* and *Bacterium*) to such forms as *Dactylothece* and *Chlorococcum,* representing capsulated forms, and *Stichococcus,* a non-capsulated form, would certainly not be overlooked, for the similarities of form and cell-grouping are certainly well marked. It is also quite possible that he would see in the gracefully curved *Raphidium* the possibilities of a *Spirosoma* or a *Spirillum.*

It seems to the writer that a consideration of the foregoing statements must at least shake the foundations of the degradation hypothesis, if not to render it highly improbable. This hypothesis is the logical outcome of the former physiological necessity of considering the first and most primitive plant forms as chlorophyll-bearing (Allen, 1895). The natural supposition was that the bacteria, saprophytic and parasitic, had originated from these chlorophyll-bearing photosynthetic ancestors. With the present physiological knowledge (Pfeffer, 1897) such a supposition concerning the primitive forms is no longer tenable, since there are bacteria that are capable of utilizing carbon dioxide (CO_2) as one of the crude substances in food manufacture without the presence of chlorophyll, and that by the process known as chemosynthesis. The first colorless forms were not dependents but were capable of leading an independent existence. In such primitive forms we have then the ancestors of the present bacteria and the blue-green algae. Starting with this chemosynthetic, non-motile, coccus form, the development of the modern bacterial branch has arisen, on the one hand, while the evolution of the Cyanophyceae has proceeded along another and somewhat parallel line. The possibility of the relation of the Protococcoideae as well as that of the Flagellata and the Chytridaceae to these primitive forms is by no means excluded.

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[1] It seems quite probable that *Bacterium viride, Bacillus virens,* and *Bacterium chlorinum,* minute chlorophyll-bearing forms, are not bacteria but primitive Protococcaceae.

It is interesting to note that in each of the suggested lines of development there are indications that the chemosynthetic mode of nutrition has been abandoned for the photosynthetic. There are undoubted flagellate infusoria that contain chlorophyll (*Phacus, Euglena*) ; the Erythrobacteria that apparently represent somewhat separated forms have made photosynthesis possible by the production of a purple pigment having chlorophyll-like properties, while the blue-green algae exhibit the typical photosynthesis of higher forms. The physiological and morphological relationship of the groups in question may be expressed as follows:

- Primitive bacterium: coccus form, non-motile, nutrition chemosynthetic.
  - Flagellata.....
    - Photosynthetic nutrition
    - Saprophytic nutrition
    - Parasitic nutrition
    - Chemosynthetic nutrition (?)
  - Haplobacteria.
    - Chemosynthetic nutrition
    - Photosynthetic nutrition
    - Saprophytic nutrition
    - Parasitic nutrition
    - Symbiotic nutrition
  - Cyanophyceae.
    - Photosynthetic nutrition
    - Saprophytic nutrition (?)
  - Trichobacteria Saprophytic nutrition only.

The relationships of the Trichobacteria must be looked upon as rather problematical. It is the opinion of the writer that they are not directly related to the Haplobacteria. If there are any bacteria that are degraded blue-green algae, they are certainly the ones, although the possibility of a direct descent from the Haplobacteria should not be absolutely excluded.

Taking into consideration the morphological characters (Migula's Classification—Migula, 1900), the phylogeny of the Haplobacteria may be expressed according to the diagram in the accompanying plate.

BIBLIOGRAPHY

ALLEN, GRANT.
1895. The Story of Plants. D. Appleton & Co.
BESSEY, C. E.
1904. Classification of the Protophyta. Trans. Am. Mic. Soc., XXV: 89–104.
BÜTSCHLI, O.
1883. Bronn's Classen u. Ordnungen des Tierreichs, I (2). 1883–1887.
1896. Weitere Ausfuhrungen über den Bau der Cyanophyceen und Bacterien. Leipzig, 1896.
CHESTER, F.
1901. Determinative Bacteriology. Macmillan Co.
COHN, F.
1875. Beitr. z. Biol. d. Pflanzen, I (3).
DE BARY, A.
1884. Morphologie u. Biologie der Pilze, Mycetozoen, u. Bakterien.
1887. Lectures on Bacteria. Clarendon Press; 1887.
FISCHER, A.
1897. Untersuchungen über den Bau der Cyanophyceen und Bakterien. Jena, 1897.
1900. Structure and Functions of Bacteria. Clarendon Press; 1900.
1905. Die Zellen der Cyanophyceen. Bot. Zeitung, LXIII: 51–129.
HALLIER, E.
1895. Pestkrankheiten der Kulturgewächse. Verlag von Erwin Nägeli; Stuttgart, 1895.
HUEPPE-JORDAN.
1899. The Principles of Bacteriology. Open Court Pub. Co.; 1899.
KOHL.
1903. Ueber die Organization und Physiologie der Cyanophyceenzelle und die mitotische Teilung ihres Kerns. Gustav Fischer; Jena, 1903.
LEHMANN-NEUMAN.
1896. Bak. Diag., 1896.
MIGULA, W.
1897. System der Bakterien, I. Gustav Fischer; Jena.
1900. System der Bakerien, II. Gustav Fischer; Jena.

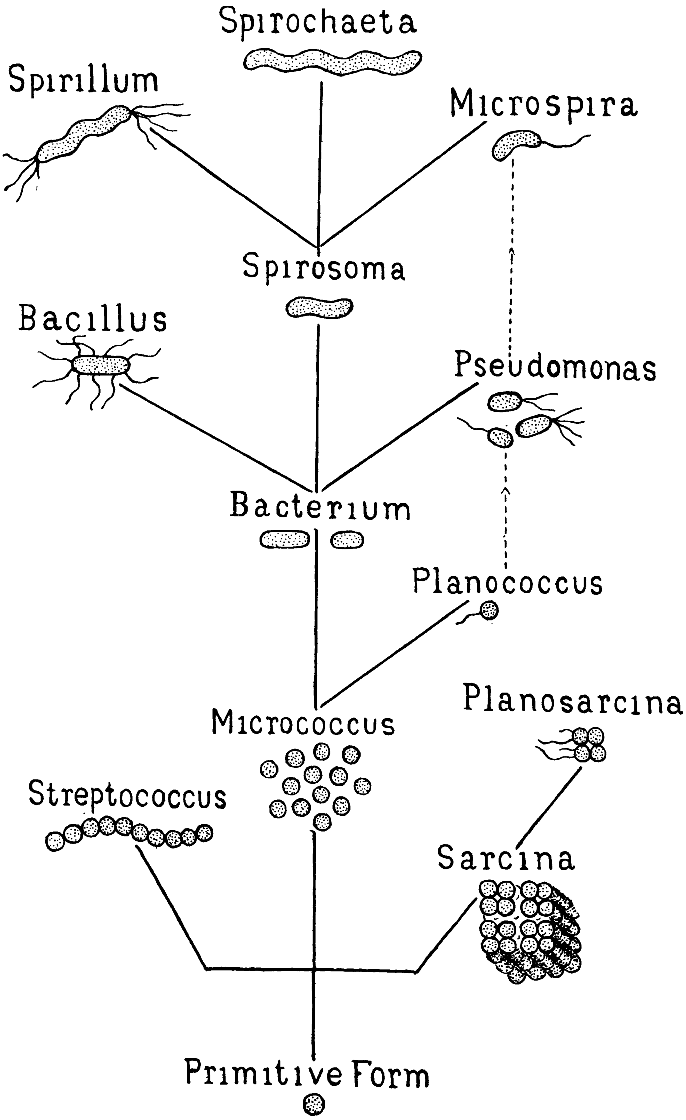
MÜLLER.
1898. Bacterien und Eumyceten. Fischer; Berlin, 1898.
OLIVE, E. W.
1904. Beihefte zum Botanischen Centralblatt, XVIII (1): 9–44.
PFEFFER, W.
1897. Pflanzenphysiologie, I. Wilhelm Engelmann; 1897.
VINES, S.
1902. Student's Text-book of Botany. Macmillan Co.; 1902.

EXPLANATION OF PLATE

Plate IV

Diagram to show the Phylogeny of the Haplobacteria.

PLATE IV


Spirochaeta
Spirillum
Microspira
Spirosoma
Bacillus
Pseudomonas
Bacterium
Planococcus
Micrococcus
Planosarcina
Streptococcus
Sarcina
Primitive Form